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The Effect of Stimulus Size on Human Cortical Potentials Evoked by Chromatic Patterns

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The effect of stimulus size on the pattern onset–offset visual evoked potential elicited with stimuli of two different wavelengths is studied under intensive yellow adaptation: (1) The onset response obtained with a 460 nm pattern is of negative polarity (N1) and saturates in amplitude with a stimulus radius of 7 deg. The onset response obtained with a 550 nm pattern is of positive polarity and continues to increase up to the maximum size (32.2 deg). (2) The peak time of N1 (460 nm) decreases with increasing stimulus size, that of P1 (550 nm) remains constant. These results are discussed as reflecting either varying retinal and brain anatomy, or cone activity, color-opponent activity, or luminance contrast activity.

S cones L cones M cones Chromatic VEP Pattern VEP Spatial summation Stimulus size

INTRODUCTION

It has been known for a long time that the occipital visual evoked cortical potential (VEP) is an electrical brain response that originates primarily from stimulation of the foveal retina while peripheral retinal areas make relatively little contributions to this response. This has been shown to be true for the unpatterned flash-evoked response (Rietveld *et al.*, 1965; De Voe *et al.*, 1968), as well as for responses evoked by patterned stimuli (Rietveld *et al.*, 1967; Harter, 1970; Behrman *et al.*, 1972; Bartl *et al.*, 1978; Groneberg, 1980; Armington & Brigell, 1981; Plant *et al.*, 1983) presented either as central disc-shaped or peripheral ring-shaped stimuli. The reason for this lies in the well known fact that the cortical projection area of the fovea is located on the convexity of the visual cortex near the brain's occipital pole and, thus, is in close proximity to the recording skin electrodes commonly employed to obtain visual responses. The mainly foveal nature of the VEP is significant in certain clinical applications. For instance, in early glaucomatous diseases which are typically associated with peripheral visual field defects the pattern-reversal VEP is relatively unaffected in its amplitude, while in advanced stages when the field defects extend into the fovea the VEP becomes significantly reduced (Ermers *et al.*, 1974; Huber, 1981; Galloway & Barber, 1981; Bartl, 1982). However, under certain stimulus precautions rod contributions originating from more peripheral retinal areas can be demonstrated also (e.g. Wooten, 1972; Adachi-Usami & Kellermann, 1973; Kojima & Zrenner, 1977).

On the other hand, as is also well known the unpatterned flash electroretinogram (ERG) may represent a mixture of both rod and cone activity with a major contribution from the retinal periphery while the central retina contributes less to the response. This is due to a different effect, namely to stray light leading to a response of the whole retina. However, if scattered light is suppressed by a strong adaptation light, photopic responses can be demonstrated which are largest upon central stimulation and fall off with increasingly peripheral stimulation (e.g. Brindley & Westheimer, 1965; Abraham & Alpern, 1984; Sandberg *et al.*, 1978). This is true also for the pattern-reversal ERG (e.g. Armington & Brigell, 1981).

It is the aim of the present investigation to examine the effects of different stimulus field sizes on the cortical pattern onset–offset VEP, obtained with two different chromatic patterns. It has been shown in an earlier investigation that with a strong yellow adaptation light either a blue or a green pattern stimulus evokes different responses which have respectively either a peak sensitivity in the blue, a long peak time, and a negative polarity, or a peak sensitivity in the yellow–green, a shorter peak time, and a positive polarity (Korth *et al.*, 1993b, 1994).

METHODS

Most of the stimulation and recording methods have been described previously (Korth *et al.*, 1993a,b, 1994) and will only quickly be reviewed here. A two-channel Maxwellian-view system (xenon arc lamp, grating monochromators) was used to provide a homogeneous

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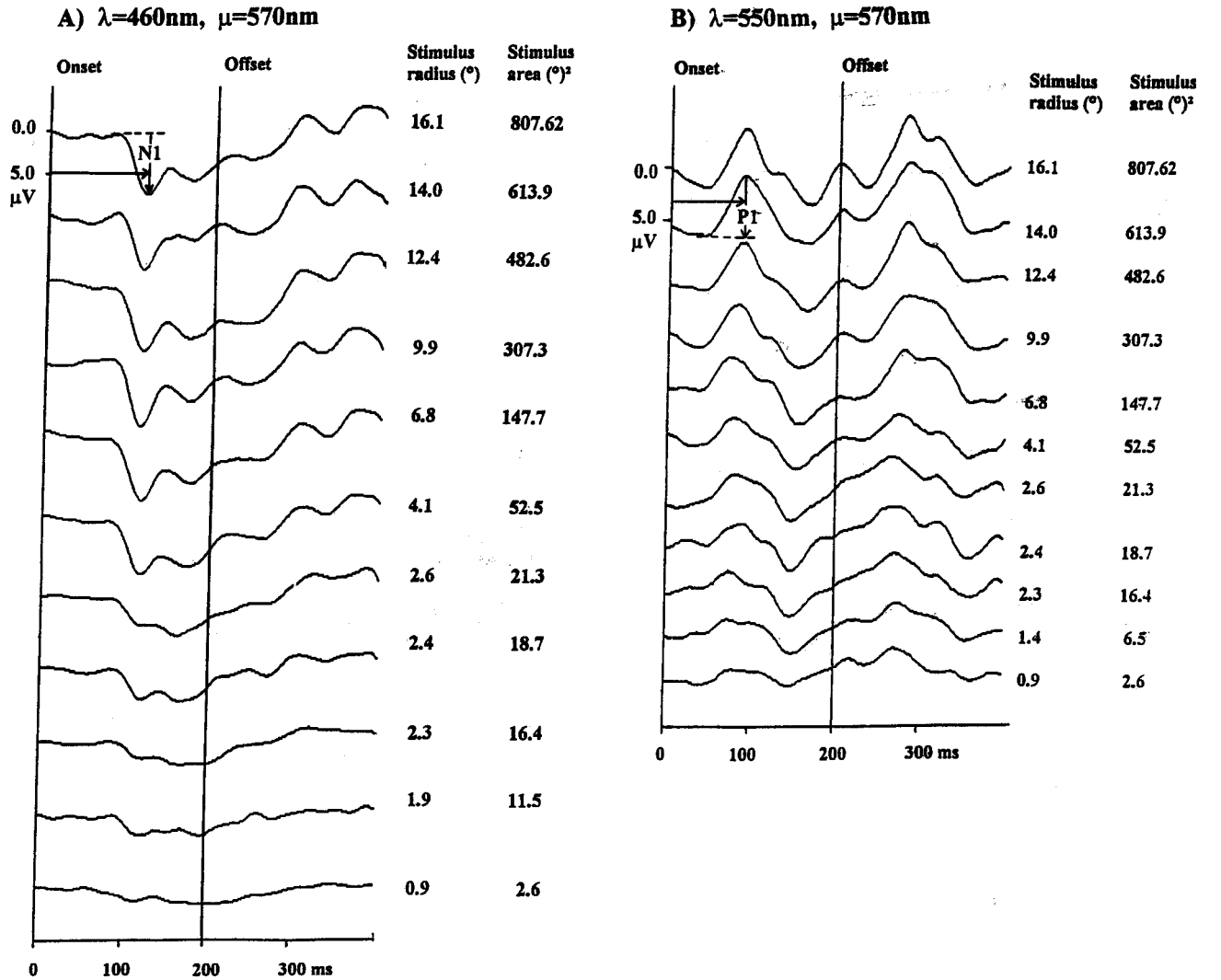

FIGURE 1. (A) Pattern onset–offset responses obtained with increasing radii of the circular field sizes. The pattern was a 460 nm, 0.88 c/deg square-wave stripe pattern presented on an unpatterned 570 nm background of high luminance. Subject SP. (B) As in (A), except that a 550 nm pattern was used. Subject SP. The vertical lines in (A) and (B) indicate the moments of pattern onset and offset, the arrows indicate the method of measurement of amplitude and peak latency of the N1 and P1 components. The records are averages of five recordings (A) and four recordings (B) with 100 sweeps each.

yellow (570 nm) background light (channel 1, 4.1 log - phot td) superimposed on a patterned light (channel 2, 2.52 log phot td) of equal size filled with either blue (460 nm) or green (550 nm) stripes. These were vertical square-wave stripe patterns which in most experiments had a fundamental spatial frequency of 0.88 c/deg. The focus in each channel could be adjusted independently by remote-controlled micromanipulators. Pattern onset–offset stimulation (Spekreijse, 1966) was accomplished by using the method of the vibrating scanner (Korth, 1983; Korth *et al.*, 1993a). The duration of the onset period was 200 msec, that of the offset period 500 msec. In Experiment 1 the diameter of both fields was adjusted to different sizes using an iris diaphragm placed behind the final lens of the viewing system. Central fixation was ensured by cross hairs. The position of the pattern within the viewing system was adjusted such that the cross hairs were always on an edge of the stripe pattern. Under this condition no change in luminance tested with a photodiode (SDC) was observed with the onset or offset of the pattern. In Experiment 2, central blanked areas in the viewing field were employed in order to provide annular stimuli with a varying inner diameter but with a constant outer diameter of 32.2 deg. These stimuli were produced by placing in the plane of the iris diaphragm thin plane sheets of glass having round spots of opaque black paint of different diameters with a tiny central pin hole in order to enable fixation. Thus, black round spots of different sizes were seen leaving blank the central parts of both the background and the stimulus field.

The VEP was recorded from the midline of the head 2 cm above the inion referenced to the contralateral ear lobe, while the ipsilateral ear lobe was grounded. A positivity of the occipital electrode resulted in an upward deflection of the records. After amplification (3 dB points at 0.5 and 30 Hz plus notch filter at 50 Hz) the EEG was averaged in a digital computer (PC AT) equipped with an AD-converter. The sampling rate was 500 Hz and 100

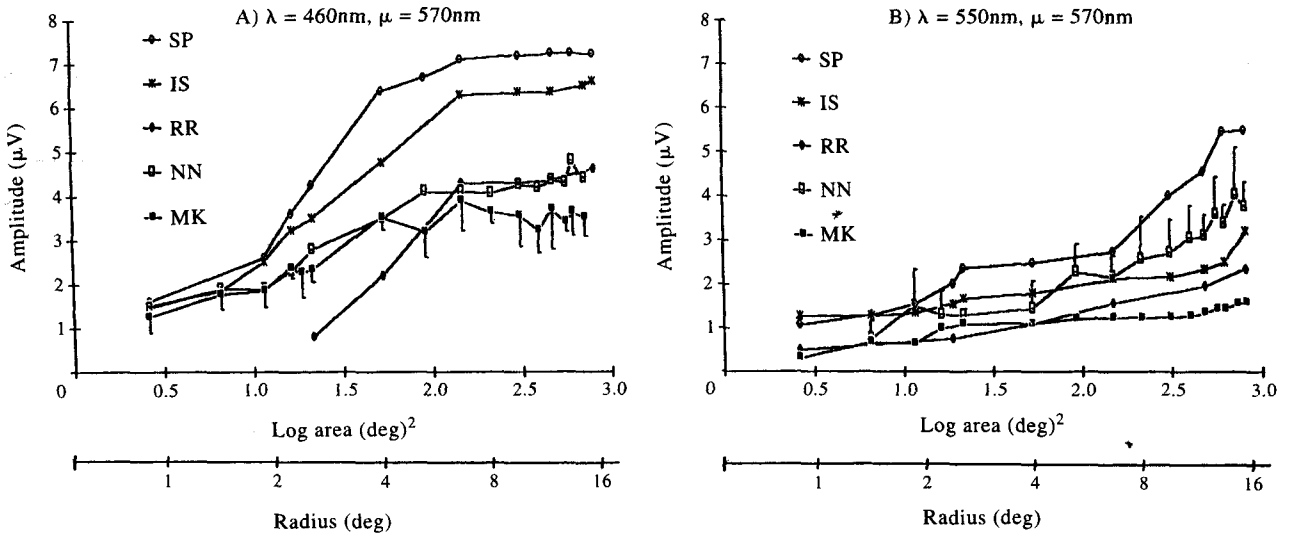

FIGURE 2. (A) Amplitudes of the onset response (N1) of five subjects obtained with the 460 nm pattern presented on the 570 nm background as a function of stimulus area. (B) Amplitudes of the onset response (P1) obtained with the 550 nm pattern as a function of stimulus size. Vertical bars in (A) and (B) indicate standard deviations calculated from five measurements.

sweeps were averaged per trial. Each trial was repeated three to five times in order to check for reproducibility or to enable a statistical evaluation. Before recording began the subject adapted to the bright stimulus field for 1 min. The amplitudes of the negative and positive response components obtained with the 460 nm and the 550 nm stimulus, respectively, were determined from the base line preceding the response to the peak of the wave. The peak times of the responses were measured from the beginning of pattern onset to the peak of the response. Five normal subjects with normal color vision (Nagel-anomaloscope, Panel D15 test, Farnsworth-Munsell 100-hue test) were examined.

RESULTS

Experiment 1: Circular stimulus field sizes

Figure 1(A) illustrates pattern onset VEPs obtained with a 460 nm, 0.88 c/deg stripe pattern of increasing stimulus field area. As can be seen, the response is mainly a negative-going, large waveform (N1) of relatively long peak time. Based on its spectral sensitivity this response has been shown previously to be initiated by the short-wave sensitive (S) cones (Korth *et al.*, 1993b). Beginning with the smallest stimulus field its amplitude increases with increasing field size but soon reaches a saturation level with no further increase. This behavior is represented graphically for the five subjects tested in Fig. 2(A). It indicates that an amplitude saturation is reached with stimulus field areas of about 148(deg)^2 (about 7 deg radius). The responses of most subjects converge to very similar amplitude values with small field sizes except for subject RR. The curve of this subject is shifted mainly rightwards to larger field sizes, although the point of amplitude saturation is the same as in the other subjects. Thus, this subject appears to be less sensitive to central blue stimuli of small sizes. The fact that the responses show no further increase with larger sizes may suggest that peripheral stimulus areas make no contribution to the responses.

In Fig. 1(B) pattern onset VEPs are shown obtained

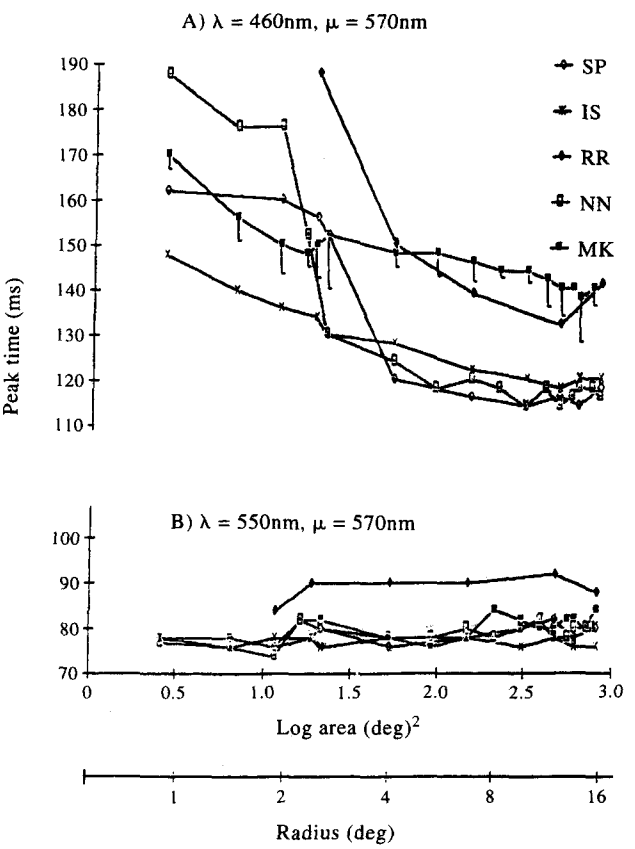

FIGURE 3. (A) Peak latencies of the N1 onset response of five subjects obtained with the 460 nm pattern presented on the 570 nm background as a function of stimulus area. Vertical error bars indicate standard deviation calculated from five measurements. (B) Peak times of the onset response (P1) obtained with the 550 nm pattern.

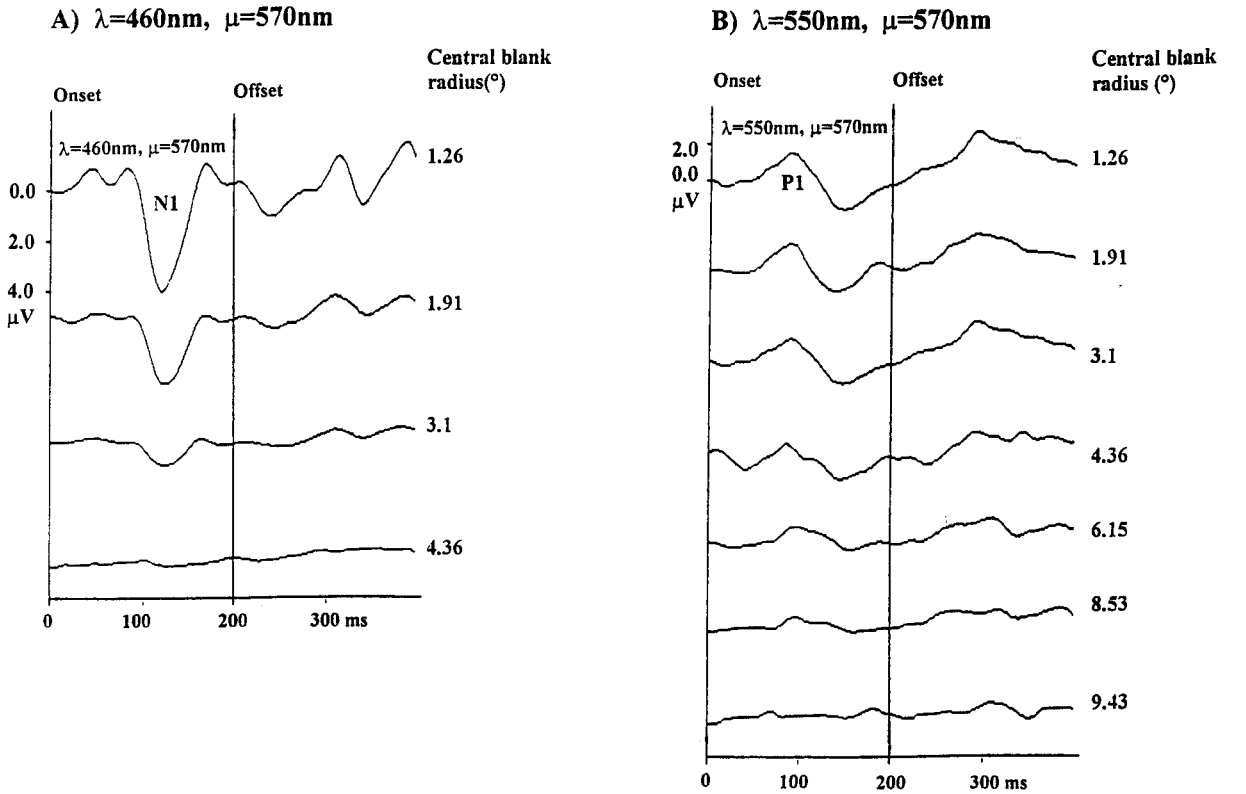

FIGURE 4. (A) Pattern onset–offset responses obtained with increasing inner radii of the annulus- or ring-shaped stimuli. The pattern was a 460 nm, 0.88 c/deg square-wave stripe pattern presented on an unpatterned intensive 570 nm background. Subject IS. (B) As in (A), except that a 550 nm pattern was used. Subject RR. The vertical lines in (A) and (B) indicate the moments of pattern onset and offset. The records in (A) and (B) are averages from three recordings with 100 sweeps each.

with a 550 nm, 0.88 c/deg stripe pattern of increasing stimulus area. Under this condition an early positive response (P1) can be seen. The spectral sensitivity has shown previously that this response originates predominantly from the activation of both the medium-wave (M) and long-wave sensitive (L) cones (Korth *et al.*, 1993b). The graphical representation of the amplitudes of this response as a function of the log of the field area [Fig. 2(B)] shows a different picture when compared with the 460 nm data of Fig. 2(A): now the response amplitudes increase steadily up to the largest stimulus field available and show no signs of saturation. This observation may suggest that with a 550 nm stimulus also the peripheral stimulus areas contribute to the responses. Figure 2 also indicates that in all subjects examined the N1 responses obtained with 460 nm are larger than the P1 components obtained with the 550 nm stimulus.

The behavior of the peak times of the responses will be considered next. Figure 3(A) shows the 460 nm data. It can be seen that with all subjects tested the peak time of the N1 component shortens with increasing field areas and approaches a more or less constant value with large field sizes. A comparison with Fig. 2(A) shows that the major changes in peak latency take place with stimulus field sizes associated with amplitude changes while with the onset of the amplitude saturation (around 7 deg) only little changes in peak latency are observed. The range of values covered by each individual can be very different. For example with subject NN the values decrease from *ca* 190 to 120 msec while for subject MK the range is from 170 to 140 msec. As one might expect from the amplitude data [Fig. 2(A)], the peak-latency curve of subject RR is displaced to larger stimulus sizes compared with the rest of the curves.

In contrast to the 460 nm curves the 550 nm data show a very different behavior [Fig. 3(B)]. Under this stimulus condition the peak latency of the P1 component does not vary in any systematic way with the stimulus field size but instead stays rather constant with values around 80 msec in most subjects. In subject RR most peak times are somewhat longer (around 90 msec).

Experiment 2: Ring (annulus)-shaped stimuli

The saturation phenomenon of the amplitude-vs-field size curves obtained with the 460 nm stimulus [Fig. 1(A) and Fig. 2(A)] suggests that visual stimuli outside a stimulus radius of about 7 deg do not evoke VEPs. To test this assumption the center of the stimulus was masked from light and only peripheral areas were stimulated. If central occlusions in the stimulus are gradually increased in diameter forming ring- or annulus-shaped stimuli of varying inner diameters and of a constant outer diameter (32.2 deg), the response amplitude should decrease and reach a zero level at a radius of about 7 deg (*ca* 148[deg]^2 stimulus area). On the other hand, with the 550 nm stimulus the response increases up to the largest available

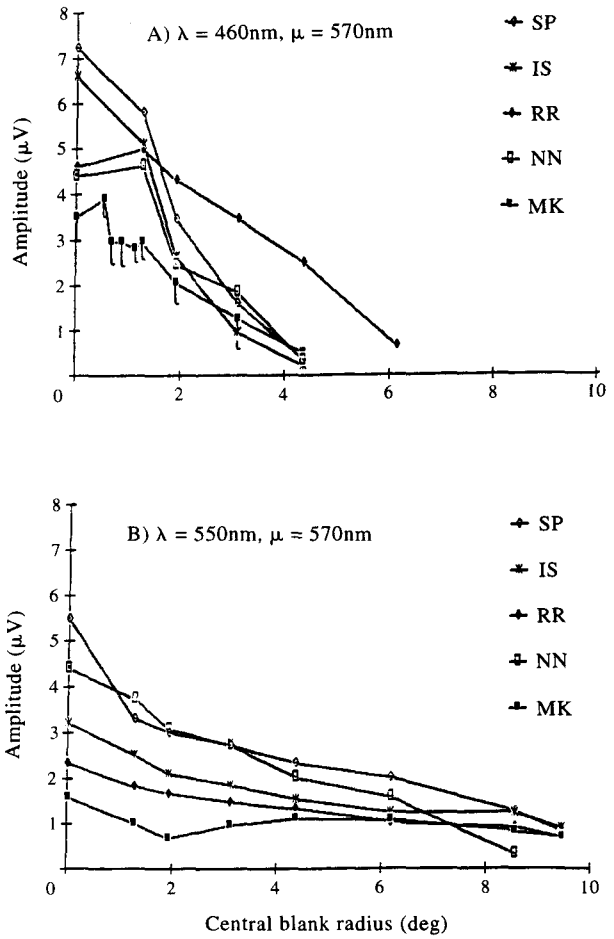

FIGURE 5. (A) Amplitudes of the onset response (N1) of five subjects obtained with the 460 nm pattern presented on the 570 nm background as a function of the inner radius of the annular stimulus. Vertical error bars indicate standard deviation calculated from five measurements. (B) As in (A), except that a 550 nm pattern was used.

field size of 32.2 deg radius, suggesting a contribution to the response also from the peripheral stimulus areas. Consequently, under this condition the response obtained with ring-shaped stimuli should decrease to zero at larger inner diameters of the annuli than with the 460 nm stimuli.

Figure 4 shows VEPs obtained with an increasing inner radius of the ring-shaped stimulus for both wavelengths tested. It is evident that with the 550 nm [Fig. 4(B)] stimulus, responses can be obtained with larger central blanked areas than with the 460 nm stimulus [Fig. 4(A)]. Thus, under the latter condition the VEP is more sensitive to blocking the central part of the stimulus. The graph of Fig. 5 which plots response amplitudes as a function of the increasing radius of the central occlusion demonstrates the results obtained under the two stimulus conditions for all subjects tested. As can be seen, the amplitudes [Fig. 5(A)] decrease at a higher rate with the 460 nm stimulus and approach the zero level at a smaller central blanked-area size than with the 550 nm stimulus [Fig. 5(B)]. As was noticed in Fig. 2(A), the 460 nm response amplitudes of subject RR showed a noticeable increase at considerably larger field areas than the rest of the subjects. From this behavior one would expect in the experiment with the ring-shaped stimuli less amplitude reduction at the smaller central occlusions. This prediction comes true in as much as this subject's response curve in Fig. 5(A) appears also to be shifted rightwards to larger inner diameters of the annular stimuli leading to higher amplitudes compared with the rest of the curves.

For the 550 nm stimulus no amplitude saturation of the P1 component could be observed [Fig. 2(B)] with the field sizes employed. Thus, the response amplitudes should converge to zero at larger central blanked areas as can be observed in Fig. 5(B). But now this limitation is not determined by a saturation phenomenon, as might be the case with the 460 nm stimulus, but by the maximum stimulus field size available.

One method for determining the local response contribution from different parts of the visual field is to divide the response amplitude by the stimulus area that is used to obtain the response and to plot this ratio as a function of increasing stimulus area or retinal eccentricity. In this way Bartl *et al.* (1978) who used a similar stimulus paradigm as in the present report, and

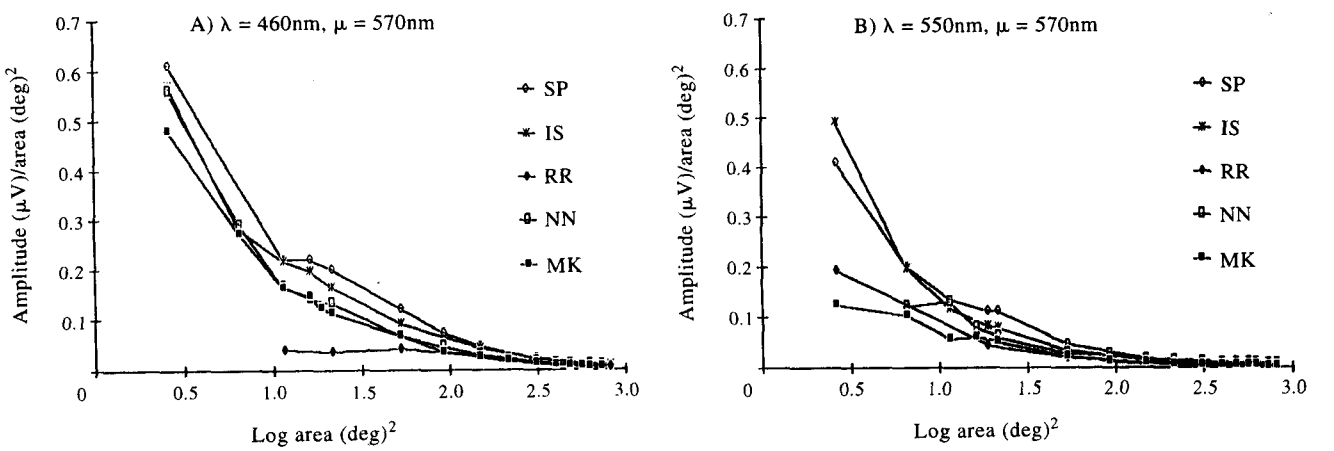

FIGURE 6. Relative responsiveness of the 460 nm (A) and of the 550 nm (B) VEP. The ratio amplitude/stimulus area was plotted as a function of the log of the stimulus area.

Armington and Brigell (1981) stimulating with concentric rings of increasing eccentricity, obtained an index of responsiveness per retinal location. A similar analysis was made with the data of the present investigation by dividing the response amplitude by the area of the stimulus field used and plotting this ratio as a function of the log of the stimulus area. Figures 6(A) and (B) show the results for the 460 nm and the 550 nm conditions, respectively. It can be seen that in general the responsiveness is largest with central retinal stimulation in most subjects and gradually falls off with larger stimulus fields for both wavelengths. For the 460 nm condition the ratios are in general higher than under the 550 nm condition since the N1 components are of larger amplitude than the P1 responses (*cf* Fig. 2). The curve of subject RR obtained with the 460 nm stimulus, however [Fig. 6(A)], shows very low ratios with a slight maximum occurring with larger stimulus fields. This verifies the suggestion of Fig. 2(A) that this subject has a low responsiveness under 460 nm stimulation with small fields.

DISCUSSION

The present VEP study which was undertaken to study areal effects with chromatic patterns led to two interesting results: (1) The 460 nm responses are mainly of negative polarity and their amplitudes saturate at a small stimulus radius of about 7 deg (148[deg]^2) while the 550 nm responses are mainly of positive polarity and increase steadily up to the largest field available (16.1 deg radius). (2) The peak times of the 460 nm responses shorten with increasing fields while those of the 550 nm responses remain constant. These results can be interpreted as reflecting either varying retinal and brain anatomy, or cone activity, color-opponent activity, or luminance contrast activity. The peak time behavior suggests different physiological mechanisms of spatial summation between two types of pathways.

The effect of the stimulus field size on the VEP amplitude has been investigated previously with colorless stimuli, either unpatterned flashes (Rietveld *et al.*, 1965, 1967; De Voe *et al.*, 1968; Kojima & Zrenner, 1976), patterned flashes (Rietveld *et al.*, 1967; Harter, 1970) or pattern-reversal (Armington, 1968; Behrman *et al.*, 1972; Bartl *et al.*, 1978; Groneberg, 1980; Röver *et al.*, 1980; Armington & Brigell, 1981; Plant *et al.*, 1983) and pattern onset–offset stimuli (Padmos *et al.*, 1973; Plant *et al.*, 1983). In studies employing patterned stimuli the spatial frequency seems to be crucial. Thus, Harter (1970) found that responses decreased with eccentric pattern flashes and that with foveal stimulation small checks (15–30 min arc) evoked the greatest amplitude, whereas in the periphery (up to 7.5 deg eccentricity) larger checks (up to 60 min arc) evoked the largest response. This was confirmed by Armington and Brigell (1981) with pattern reversal stimulation. This suggested that the receptive field organization played an important role. Rietveld *et al.* (1967) working with flashed patterns of 20 min arc checks found for a certain response component an amplitude saturation with a field size of about 3 deg. Armington (1968) found with a much coarser pattern-reversal stimulus (1 c/deg stripes) a linear relationship between response amplitude and stimulus size up to the largest field diameter (12 deg). Behrman *et al.* (1972) found with small check sizes (9 min arc, pattern reversal) an amplitude saturation with small fields (between 1 and 2 deg) while with coarse patterns saturation occurred at larger field sizes or was not observed at all (35 min arc). Similar observations were made by Groneberg (1980) for pattern reversal and by Plant *et al.* (1983) for reversal and onset stimuli. In addition, Groneberg (1980) and Plant *et al.* (1983) found that the amplitude tuning of the VEP occurred with a large stimulus field at larger checks and with a small field at smaller checks, again a finding explained on the basis of different receptive field organizations. Interestingly, with pattern onset–offset stimulation Padmos *et al.* (1973) observed in the monkey no amplitude saturation with a 24 min arc check size, while with an unpatterned stimulus saturation set in at 6 deg field diameter. Plant *et al.* (1983) found a linear relation between the spatial frequency of a luminance-contrast stripe pattern and the log of the stimulus area at which amplitude saturation of the P1- and N1-onset- and reversal responses occurred. According to them an amplitude saturation with a 0.88 c/deg pattern should occur beyond a field size of 32.2 deg diameter as used here. However, in the present experiment two different mechanisms were studied which could interact with spatial tuning in different ways. It will be argued below that the P1 potential in the 550 nm response is probably a luminance-contrast or M-cell type component which shows a spatial low-pass behavior (Korth *et al.*, 1988; Previc, 1988). For this response a low spatial frequency seems to lead to increasing amplitudes with very large fields, while a high spatial frequency might lead to saturation with smaller fields. On the other hand, the N1 component in the 460 nm response could be a chromatic or P-cell type response (see below) which generally shows a spatial band-pass behavior (Murray *et al.*, 1987; Korth *et al.*, 1988; Previc, 1988). With the presently used stimulation the S cone initiated VEP has its spatial tuning at relatively low spatial frequencies (Korth *et al.*, 1993b) and it is uncertain what the amplitude saturation would be with other spatial frequencies.

The behavior of the VEP response peak time has been studied less intensively. Van Balen *et al.* (1966) and De Voe *et al.* (1968) reported smaller and delayed responses with peripheral flashes. Rietveld *et al.* (1965, 1967) found that certain response components varying in peak time with the luminance of unpatterned and patterned flashes do not do so with varying stimulus field size, while other components decrease in peak time with increasing light flux, independent of whether this is due to stimulus luminance or size. De Voe *et al.* (1968) observed with unpatterned flashes of small areas (up to 2 deg 40 min arc) faster responses with increasing luminance as well as stimulus size. Area-intensity data derived from luminance curves for a constant criterion peak time resulted in

threshold curves which were very similar to psychophysical thresholds obtained under the same stimulus conditions. Kojima and Zrenner (1976) using the same paradigm under scotopic conditions with stimulus field diameters up to 110 deg found spatial integration to occur in both psychophysical and VEP measurements over the whole range of stimulus sizes. Adachi-Usami and Kellermann (1973) observed spatial summation in the scotopic VEP for a stimulus diameter of at least 18 deg. The peak-time data of Fig. 3 suggest that with the 550 nm stimulus no spatial integration occurs while with the 460 nm stimulus, summation can be followed up to a radius of about 7 deg, the point where amplitude saturation sets in [Fig. 2(A)]. Whether peak-time changes occur in the 550 nm pattern-onset VEP for very small stimulus sizes (<1 deg) as examined by De Voe *et al.* (1968) has not been tested in the present experiment. Thus, with respect to spatial integration the 460 nm response behaves similar to the rod response, while the 550 nm response integrates probably over only a very small area and parallel processing might occur with larger stimulus field sizes.

The discussion of the present data obtained with chromatic stimuli has different aspects pertaining to the question whether the responses reflect cone activity, chromatic color-opponent activity, or luminance-contrast mechanisms. It has been shown before (Estevez *et al.*, 1975) that the VEP which is recorded from a late stage of processing can in fact reflect the activity of different cone types. If this were true also with the present data, the differences in the response-amplitude functions observed with the two wavelengths (Fig. 2) could be based on the different anatomical distribution of S, L, and M cones across the retina. It has been shown (Marc & Sperling, 1977; De Monasterio *et al.*, 1981, 1985) that in the primate the density of the L and M cones is highest in the foveola and falls off towards the periphery. The density of the S cones, on the other hand, is highest at about 1 deg eccentricity and drops sharply towards the foveola and falls gradually towards the periphery. In addition, the proportion of the S cones is much lower (about 12–14% between eccentricities of 5 and 40 deg) than that of the L and M cones. If this applied also to the human, it might in part explain the amplitude saturation of the N1 component with increasing field sizes [Fig. 1(A) and Fig. 2(A)]: if the cone density falls below a certain value the response initiated by them could be too low to be detected in the VEP. This seems to occur at an eccentricity of about 7 deg in the human where in the primate the S cone density is about $2.25 \times 10^3/\text{mm}^2$ (Marc & Sperling, 1977) to $9 \times 10^2/\text{mm}^2$ (De Monasterio *et al.*, 1981). The L plus M cone density, on the other hand, remains far above this level for eccentricities up to 40 deg, thus explaining the continuing increase of the P1 component.

The decrease in S cone density towards the foveola as observed by Marc and Sperling (1977) and De Monasterio *et al.* (1981, 1985) could not be demonstrated in the present study since responses originating from retinal areas below 1 deg radius become too small to be reliably detected in the VEP. In addition, the spatial frequency used may not be optimal to demonstrate the "foveal tritanopia" (König, 1894; Wald, 1967; Williams *et al.*, 1981) since one cycle of the stripe pattern used has a width of 1.14 deg of visual angle. The use of a finer pattern might be more appropriate for the examination of small foveal areas.

However, when VEP amplitude is used to measure cone responses as a function of stimulus size, not only retinal anatomy and cortical representation but also other secondary factors become important like e.g. macular pigmentation and chromatic aberration. The effect of macular pigment absorption relative to 460 nm has recently be shown psychophysically using a blue-on-yellow stimulus paradigm to be 0.4 log units at the foveola while it was negligible at 5.5 deg eccentricity (Wild & Hudson, 1995). This would mean that with the 460 nm pattern as used here the response curves of Fig. 2(A) might be attenuated especially with the small field sizes. As mentioned above and as expressed in several figures, the data obtained under the 460 nm condition from subject RR deviate from the rest of the subjects although this subject did not show any blue-color vision anomalies. In order to understand this deviation a different retinal anatomy could be considered like a larger central area free of S cones (extended tritanopia) or a high density of the macular pigment. In addition, since the VEP, although dependent on retinal receptors, is generated by cortical neurons the high inter-subject variability of the expression of the central visual field on the convexity of the cortex at the occipital pole (Brindley, 1972) must be considered. Thus, a source of error in the present experiments might be introduced because various response components summate and cancel depending on individual cortical representation and consequent topographic potential distribution. Also, spatially extensive stimuli can produce additional stimulus intrusions due to chromatic aberration (Robson & Kulikowski, 1995).

The possibility must be considered that the present data could reflect either chromatic or achromatic (luminance contrast) mechanisms in the brain. Previous reports have shown that not only yellow but also white backgrounds are able to disclose opponent-color contributions to visual detection. The balance between the chromatic mechanisms can be altered depending on whether yellow or white is used for adaptation and depending on the color temperature of the white (Nacer *et al.*, 1995). Furthermore, with a white background a change from a chromatic to a luminance mechanism can be observed when the size or the duration of the test flash is reduced (King-Smith & Carden, 1976). With respect to the VEP it has been shown that a main component of pattern-onset responses elicited with isoluminant chromatic-contrast gratings is of negative polarity while with luminance-modulated (achromatic) patterns it is of positive polarity (Carden *et al.*, 1985; Murray *et al.*, 1987; Korth *et al.*, 1988; Berninger *et al.*, 1989; Murray & Parry, 1989; Kulikowski *et al.*, 1989; Regan & He,

1996). This suggests that the neurophysiological processing of chromatic and achromatic information is reflected by opposite polarities of the main component of the onset VEP. If this were a general rule, the possibility must be considered that the 460 nm responses being of negative polarity [Fig. 1(A)] reflect a chromatic mechanism although the stimulus was not a typical isoluminant chromatic-contrast pattern. On the other hand, the present findings could argue against this rule.

In the case of a 550 nm pattern on a 570 nm background both wavelengths are located on either side of a perceptual boundary in the spectrum necessary for a color discrimination task (Mullen & Kulikowski, 1990), however, the two wavelengths may not be optimal with respect to the spectral centroids (Jordan & Kulikowski, 1995). In addition, the fact that the 550 nm pattern evokes responses of positive polarity [Fig. 1(B)] suggests that the responses are produced by an achromatic luminance mechanism. Furthermore, the onset responses obtained with large stimulus areas are virtually identical in wave shape to the offset responses [Fig. 1(B)] supporting the notion that these responses are generated by luminance detectors (Kulikowski, 1977). Finally, the peak of the spectral sensitivity of positve responses studied with the same background (Korth *et al.*, 1993b) lies close to the peak of the photopic luminosity, or V-Lambda, function for which the phasic magnocellular cell system is likely to provide the underlying mechanism (Lee *et al.*, 1988; Lee & Martin, 1989). Thus, the behavior of the 550 nm responses with increasing field size [Fig. 2(B)] could be applicable also to achromatic VEPs whose positive component is likely to reflect M-cell function (Previc, 1988). However, even this is not quite certain since the onset–offset symmetry of the 550 nm responses [Fig. 1(B)] is nearly complete only with large stimulus fields while with small fields (below about 4 deg radius), excluding more magnocellular neurons, this is less clear. Thus, a mixture of chromatic and achromatic responses cannot be excluded with small stimulus fields.

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